Elytra, Tokyo, **33** (1): 245–257, May 30, 2005

Diurnal Activity of the Japanese Stag Beetle *Prosopocoilus dissimilis okinawanus* NOMURA (Coleoptera, Lucanidae)

Yoshihito HONGO

Entomological Laboratory, College of Agriculture, University of the Ryukyus, Nishihara, Okinawa, 903–01 Japan[1)]

Abstract A previous study demonstrated that adults of the Japanese stag beetle *Prosopocoilus dissimilis okinawanus* of the northern population (Yanbaru population) on Okinawa Island are nocturnal. However, in the southern population (Naha population) of *P. d. okinawanus*, diurnally active adults were observed in my pilot survey. To confirm the daily activity pattern of them, activity of adult *P. d. okinawanus* of the Naha population was examined in the field and laboratory throughout a day. In the field, *P. d. okinawanus* of the Naha population was observed to be active diurnally as well as nocturnally, but it was much more active nocturnally than diurnally in the laboratory. I discuss why *P. d. okinawanus* of the Naha population is active not only in the nighttime but also in the daytime, contrary to the nocturnally active Yanbaru population, from the viewpoint of the difference in food plants for adults between these two populations.

Introduction

Adults of *Prosopocoilus dissimilis okinawanus*, which is distributed on Okinawa Island, Japan, often aggregate on citrus fruit trees to lick sap exuding on the tree surface (*e.g.*, OKAJIMA & YAMAGUCHI, 1988; HORI, 1996). SHIOKAWA and IWAHASHI (2000 b) surveyed the daily activity of *P. d. okinawanus* found on sap exuding sites of citrus fruit trees in a small grove located in a subtropical broadleaved forest in the northern part of Okinawa Island and reported clear differences in male reproductive behavior among the three morph groups (L, S1, and S2 types: see Materials and Methods, Fig. 2), which is similar to alternative reproductive behavior known in the Japanese horned beetle (SIVA-JOTHY, 1987). In addition, they showed that females and all three morphs of males in that population were basically nocturnal.

In isolated patches of small woods left in city areas, adults of *P. d. okinawanus* usually aggregate at the tip of branches of *Clerodendron trichotomum* var. *esculentum* (HONGO, 2001) and *Persea thunbergii* (HORI, 1996; HONGO, 2001). In the case of *Citrus depressa*, which is the commonest citrus fruit tree cultivated mainly in northern

1) Present address: Department of Zoology, Graduate School of Science, Kyoto University, Kitashirakawa, Sakyo, Kyoto, 606–8502 Japan.

part of Okinawa Island (Ogimi Village) and is used by adults of *P. d. okinawanus* as food resource, sap is often exuding from wounds of trunks that are considered to be caused by boring insects (HONGO, personal observation) and beetles simply lick sap already available on the surface of trunks. On the other hand, in the case of *C. trichotomum* var. *esculentum* and *P. thunbergii*, there were rarely wounded trunks that produce exuding sap. Thus, beetles that aggregate on these plants are obliged to gnaw the bark of branches off to exude sap using their own mandibles like nippers (Fig. 1; see also HONGO, 2001). Therefore, ecological conditions for adult *P. d. okinawanus* are quite different due to the difference of habitats.

It has been well known that geographically isolated populations of a species often have different morphology and behavior, reflecting local adaptations to different ecological conditions (*e.g.*, KREBS & DAVIES, 1993; FOSTER & ENDLER, 1999). Thus, it is possible that the differences of ecological conditions between populations of *P. d. okinawanus* could cause some behavioral differences between them. Actually, during a pilot survey in a population inhabiting small woods left in a city area of the southern part of Okinawa Island, I observed diurnally active individuals, including copulating pairs, of *P. d. okinawanus*, which is a quite different phenomenon from that observed by SHIOKAWA and IWAHASHI (2000 b) in the northern population. Except for the study of this northern population, however, there is no report on daily activity of *P. d. okinawanus* observed throughout a day. Here, I report on the field and laboratory observations of the daily activity pattern of *P. d. okinawanus* in a southern population inhabiting a graveyard in Naha City.

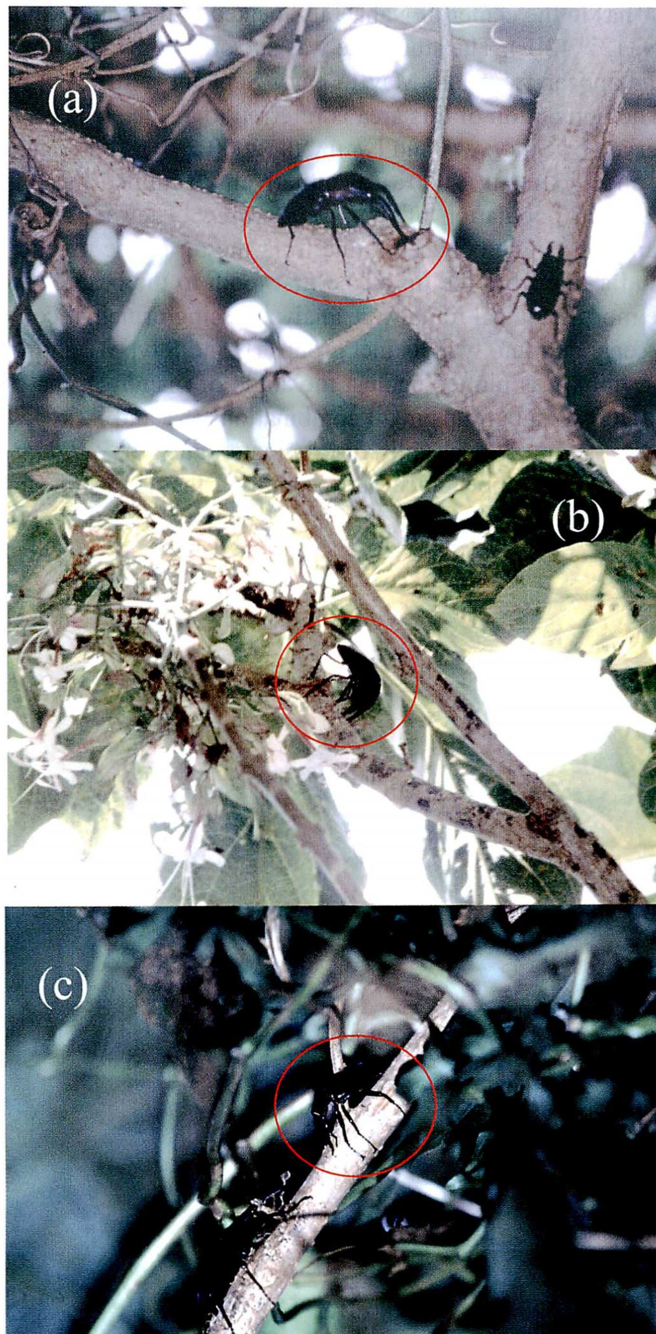
Because the existence of alternative reproductive behaviors corresponding to morphological alternatives has been recognized in males of *P. d. okinawanus* (SHIOKAWA & IWAHASHI, 2000 b), it is expected that males of the southern population also exhibit intraspecific variation in male reproductive behavior. Furthermore, if the differences of ecological conditions between the two populations of *P. d. okinawanus* cause some differences in daily activity patterns between them, it is possible that males of *P. d. okinawanus* in the southern population may show reproductive behavior different from that of the northern one. Thus, I also report daily patterns of mating activity of wild *P. d. okinawanus* in the southern population.

Materials and Methods

Male morphological types

Field survey and beetle sampling for laboratory observation were conducted at the

Fig. 1. Bark gnawing behavior of L type (a), S2 type (b) and S1 type males of *Prosopocoilus dissimilis okinawanus* (surrounded by red circles). Beetles on the surface of bark of *Clerodendron trichotomum* var. *esculentum* or *Persea thunbergii* bend their head down and stick mandibles into bark, then repeatedly pinch it. As a result of this behavior, bark is slightly stripped and sap exudes from these scars temporarily.


(a)
(b)
(c)

graveyard (ca 50 ha) in the center of Naha City located in the southern part of Okinawa Island (26°13′N, 127°42′E). The study site was surrounded by small woods. Adults of *P. d. okinawanus* appear from late May to early September (*e.g.*, OKAJIMA & YAMAGUCHI, 1988). The population of this area is referred to as the Naha population and the population observed by SHIOKAWA and IWAHASHI (2000 a, b) as the Yanbaru population.

SHIOKAWA and IWAHASHI (2000 a) quantitatively examined the polymorphism of males in the Yanbaru population of *P. d. okinawanus*. They reported that when the angle of the mandible (angle between a line from the tip of the mandible to the tip of the first tooth and a line from the tip of the first tooth to the base of the mandible) in addition to nine morphological traits were analyzed using principal components analysis, males were separated into two distinct groups (L and S types), and when the size of each of the nine traits was plotted against the angle of mandible, males of the S type were separated into two subgroups in all combinations (S1 and S2 types). On the basis of these criteria I attempted to visually discriminate males of *P. d. okinawanus* of the Naha population by their appearance and categorize them into the three morphs. If

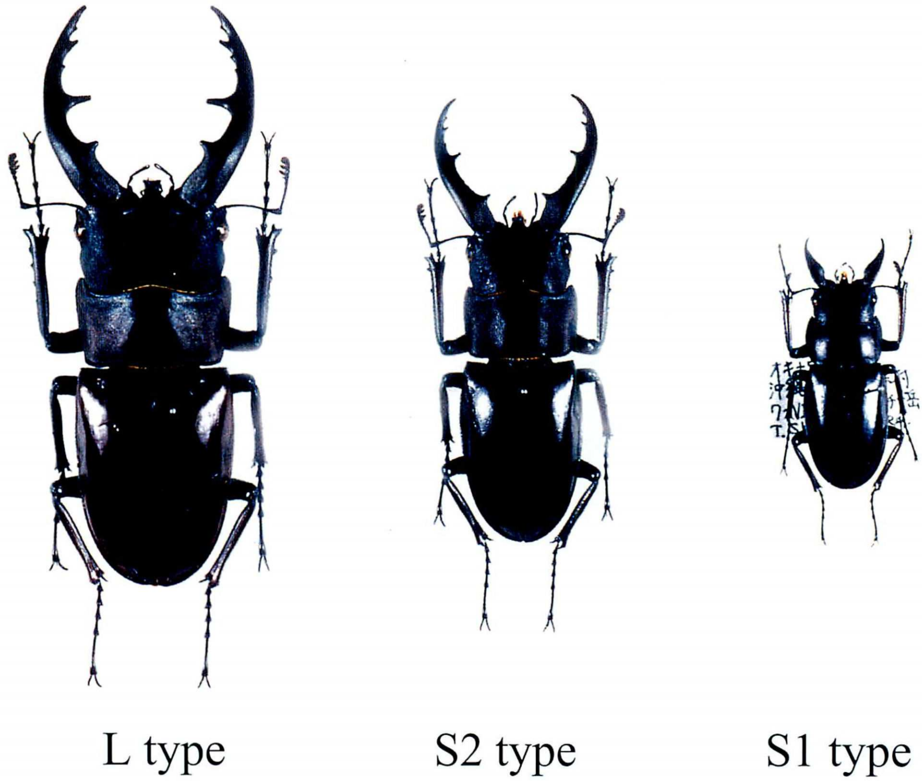


Fig. 2. Typical three male morphs of *Prosopocoilus dissimilis okinawanus* (specimens were furnished by T. SHIOKAWA).

there were any individuals of ambiguous size that could not be clearly categorized (less than 3% of individuals during one observation period in the field), I excluded them from data in order not to categorize them arbitrarily. According to SHIOKAWA and IWAHASHI (2000 a), large individuals were defined as the L type, and larger and smaller groups of small individuals were defined as the S2 and S1 types, respectively (Fig. 2).

Field observations of daily activity

I selected fifteen trees (13 *Clerodendron trichotomum* var. *esculentum* and two *Persea thunbergii*) as survey trees. To examine the daily activity pattern of adults of *P. d. okinawanus* throughout a day, observations were carried out from 20:00 to 18:00 of the subsequent day on 26–27 June, 3–4 July, and 15–16 July 1999. The average temperature during three observation periods was 27.4°C. The numbers of sighted individuals and mating individuals found on the survey trees and their sex and type were recorded every two hours. I did not individually mark beetles because, if beetles are captured for marking, they would escape immediately after releasing and rarely come back to feeding spots due to some kinds of disturbance (SHIOKAWA & IWAHASHI, 2000 b).

Laboratory observations of daily activity

Transparent plastic cage (40×70×40 cm deep) was used for laboratory observations. The cage was filled with leaf mold up to ca 10 cm from the bottom, and approximately ten leaves of *C. trichotomum* var. *esculentum* and three perches of *Quercus acutissima* (length: 20 cm, diameter: 10 cm) were provided as shelters on the leaf mold. Insect Jelly (Fujikon®) (the internal cubic volume per one jelly is 16 g) was put in two feeding spots of each perch of *Q. acutissima* as food. Beetles captured from 22 July to 20 August 1999 at the study site were individually marked on their elytra with quickly drying paints (Mitsubishi Paint Marker®), and three males of L, S1, and S2 types each and three females (totally 12 individuals) were introduced into the cage. To acclimate to the condition, beetles were kept undisturbed in the cage for at least 24 hours in the laboratory, where photophase was set from 5:30 to 19:30 with constant air temperature at 25°C, which was similar to the average temperature during the field observation periods. Observations of daily activity were conducted from 20:00 to 18:00 of the subsequent day on 28–29 July and 5–6, 14–15, and 26–27 August. In each observation, two cages were prepared, resulting in a total of eight trials. The number of appeared individuals (individuals not hiding under shelters) and their sex and type were recorded every two hours during the trial. Beetles used for each trial were captured within a week prior to each trial. All beetles and all jellies were exchanged after each trial. Observations during the dark period were carried out with a flashlight covered with red cellophane to minimize the disturbance to beetles.

Results and Discussion

Daily activity

It is possible that differences of observation periods would affect the daily activity pattern. However, activity patterns did not show significant differences among the three field observation periods in both males and females (Table 1) (males: 12×3 contingency table analysis, $\chi^2=13.90$, $p=0.905$; females: 4×3 contingency table analysis, $\chi^2=2.27$, $p=0.893$). Therefore, the data of the three observation periods were pooled in the following analyses.

Figure 3 shows the numbers of males of each type and females found every two hours in the field. Females and all types of males were observed throughout a day. Six L type males were found at 20:00, then the number of L type males increased rapidly, showing a peak during the night at 22:00. After that the number of them decreased gradually until sunrise and began to increase again, achieving the daily maximum peak (19 individuals) at 8:00. The number of S2 type males fluctuated between six and 12. Contrary to L type males, appearance of S1 type males achieved the daily maximum individual number (22) during the nighttime at 2:00. On the other hand, the number of females showed two peaks, just after the sunset at 20:00 (16 individuals) and just before the sunrise at 4:00 (14 individuals). Comparisons of the average number of observed individuals per two hours between nighttime (20:00–6:00) and daytime (6:00–20:00) showed no significant differences between them in both males (all types combined) and females (Table 2). When the comparisons were made for the three types of males separately, the number of S1 type males was significantly larger in the nighttime

Table 1. The numbers of observed males and females of *Prosopocoilus dissimilis okinawanus* recorded every two hours in three field observation periods.

	Number of males											
Observation period	Time of day											
	20	22	0	2	4	6	8	10	12	14	16	18
26–27 June	5	6	9	9	11	9	8	11	11	3	3	4
3–4 July	17	21	22	15	18	21	19	22	17	15	11	10
15–16 July	7	8	13	10	9	10	10	5	5	5	8	6
	Number of females											
Observation period	Time of day											
	20	22	0	2	4	6	8	10	12	14	16	18
26–27 June	4	3	4	3	5	4	2	6	6	2	2	2
3–4 July	10	4	5	7	7	9	10	7	7	5	6	6
15–16 July	2	1	2	2	2	2	1	1	1	2	1	1

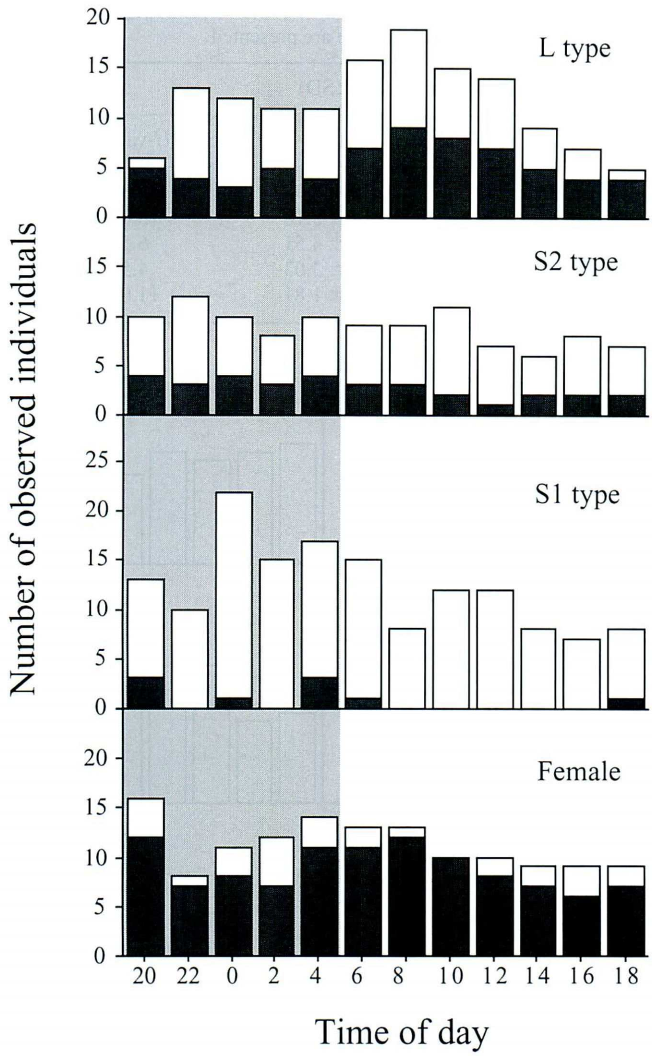


Fig. 3. The numbers of observed individuals and matings (black bars) in males (L, S2, and S1 types) and females of *Prosopocoilus dissimilis okinawanus* recorded every two hours in the field. The data of three observation periods were pooled. Shadow part indicates nighttime. See Fig. 2 for L, S2, and S1 types.

than in the daytime (Table 2). There were no significant differences in S2 type males, although the difference was marginally non-significant. The number of L type males showed no significant differences between the nighttime and daytime.

Figure 4 shows the number of males of each type and females appeared every two hours in the laboratory. The data of the four trials were pooled because appearance patterns of beetles did not significantly differ among the four trials in both males and fe-

Table 2. The numbers of adult *Prosopocoilus dissimilis okinawanus* observed in the field. Average numbers per two hours for the nighttime and daytime are presented.

Sex/type	No. of individuals (mean±SD)		*U*-test	
	Nighttime	Daytime	*U*-value	*P*-value
Male (total)	36.00 ± 5.52	30.28 ± 8.38	11.50	0.33
L type	10.60 ± 2.70	12.14 ± 5.18	13.00	0.46
S2 type	10.00 ± 1.41	8.14 ± 4.51	6.50	0.07
S1 type	15.40 ± 4.51	10.00 ± 3.03	4.50	0.03
Female (total)	12.20 ± 3.03	10.43 ± 1.81	11.00	0.29

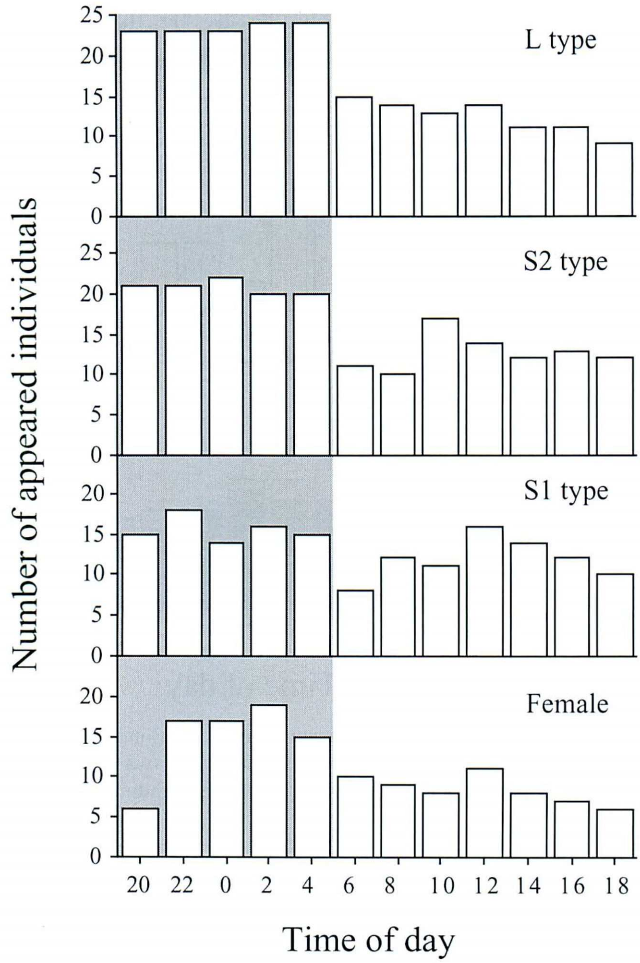


Fig. 4. The numbers of appeared males (L, S2, and S1 types) and females of *Prosopocoilus dissimilis okinawanus* recorded every two hours in the laboratory experiment. The data of four trials were pooled. Shadow part indicates nighttime. See Fig. 2 for L, S2, and S1 types.

Table 3. The numbers of appeared males and females of *Prosopocoilus dissimilis okinawanus* recorded every two hours in four laboratory observation periods.

Observation period	Number of males											
	Time of day											
	20	22	0	2	4	6	8	10	12	14	16	18
28–29 July	13	15	15	15	15	8	9	12	12	12	10	12
5–6 August	14	17	14	13	15	9	9	10	11	9	7	6
14–15 August	16	15	16	16	17	10	9	8	10	9	9	6
26–27 August	16	15	13	16	14	8	9	10	11	8	8	7
	Number of females											
Observation period	Time of day											
	20	22	0	2	4	6	8	10	12	14	16	18
28–29 July	0	5	2	4	2	2	3	3	5	2	2	2
5–6 August	2	4	5	6	5	4	3	4	4	4	3	3
14–15 August	1	4	4	4	4	2	1	1	1	1	1	0
26–27 August	3	4	6	5	4	2	2	0	1	1	1	1

Table 4. The numbers of active adult *Prosopocoilus dissimilis okinawanus* recorded during the laboratory observation. Average numbers per two hours for the nighttime and daytime are presented.

Sex/type	No. of individuals (mean±SD)		*U*-test	
	Nighttime	Daytime	*U*-value	*P*-value
Male (total)	59.80 ± 1.30	37.00 ± 4.32	0.00	0.004
L type	23.40 ± 0.55	12.43 ± 2.15	0.00	0.004
S2 type	20.80 ± 0.84	12.71 ± 2.29	0.00	0.004
S1 type	15.60 ± 1.52	11.86 ± 2.61	4.00	0.03
Female (total)	14.80 ± 5.12	8.43 ± 1.72	6.50	0.07

males (Table 3) (males: 12×4 contingency table analysis, $\chi^2=6.68$, $p>0.999$; females: 4×4 contingency table analysis, $\chi^2=12.86$, $p=0.169$). Although females and all types of males appeared throughout a day, they all showed the maximum individual numbers during the night (L type: at 2:00 and 4:00; S2 type: at 0:00; S1 type: at 22:00; female: at 2:00). When the average number of appeared individuals per two hours was compared between the nighttime and daytime, the numbers of males of each type were significantly larger in the nighttime than in the daytime (Table 4). Average number of females was also larger in the nighttime than in the daytime, although the difference was marginally non-significant (Table 4).

Females and all types of males of *P. d. okinawanus* in the Naha population were observed throughout a day in the field. There were no significant differences in the average number of observed individuals per two hours between the nighttime and daytime in both males and females. On the contrary, in the Yanbaru population of *P. d. okinawanus*, SHIOKAWA and IWAHASHI (2000 b) have reported that all types of males and females showed nocturnal activity throughout observations of two successive nights (10–11 and 14–15 July). In their study, however, it cannot be ascertained that *P. d. okinawanus* is active only in the nighttime because the observation was started at 18:00 and was terminated at 9:00. Nevertheless, in their study females and all types of males began to appear from 18:00 after sunset and showed clear declining tendencies after 5:00, and hence it would be safe to say that *P. d. okinawanus* of the Yanbaru population is nocturnal. In the present study, under the laboratory conditions females and all types of males exhibited higher activities during the nighttime than the daytime.

Why *P. d. okinawanus* of the Naha population is active not only in the nighttime but also in the daytime in the field? And why *P. d. okinawanus* of the Naha population is more active in the nighttime than in the daytime under the laboratory conditions? One possible reason is a difference of the amount of available food per unit time for beetles between the two populations. In a case of the oak tree, *Quercus acutissima*, it was reported that sap exudation is promoted due to boring by carpenterworms under bark (YOSHIMOTO & NISHIDA, 2004). It is likely that beetles of the Yanbaru population can obtain sufficient amount of food, because *C. depressa*, a food plant for them, often produce sap exuding wounds on trunks that is considered to be caused by boring insects (HONGO, personal observation). On the other hand, it is likely that beetles of the Naha population cannot obtain sufficient amount of sap because food plants in this population *C. trichotomum* var. *esculentum* and *P. thunbergii*, do not produce sap unless beetles themselves strip the bark off by gnawing with their mandibles (Fig. 1; see also HONGO, 2001). Actually, I observed 13 cases of this bark gnawing behavior during the present field observations (6, 4, and 3 cases in L, S2, and S1 type males, respectively). It may be assumed that this difference of food availability may induce *P. d. okinawanus* of the Naha population to be active in the daytime as well as in the nighttime, because beetles cannot take enough amount of food if they are active only during the nighttime. In the present laboratory observation, it is possible that beetles were less active during the daytime because the conditions of food availability was better compared to the natural conditions. To test this assumption, studies on the amount of sap exuding in food plants of *P. d. okinawanus* and laboratory experiments with various food availability conditions are necessary.

Another possible reason is the difference of temperature between field and laboratory. In *Chironomus yoshimatsui*, it has been known that the timing of daily activity is affected by seasonal change of temperature conditions (KON, 1984). In the present study, the observation in the field was conducted approximately one month earlier than the laboratory tests. Although the difference of mean temperature between the field (27.4°C: average) and the laboratory (25°C: constant) was small, it may have caused

some difference in daily activity patterns between them.

Mating behavior in the field

Mating individuals were observed throughout a day except for S1 type males (Fig. 3). The number of mating L type males showed the maximum peak (nine individuals) at 8:00 just after the sunrise, when highest frequency of mating females was observed. The number of mating S2 type males fluctuated between one and four. In S1 type males, three mating individuals were recognized at 20:00 and 4:00, and one individual at 0:00, 6:00 and 18:00. On the other hand, the number of mating females showed two peaks at 20:00 and 8:00 (13 individuals each). When the average number of observed mating individuals per two hours was compared between the nighttime and daytime, the number of mating L type males was larger in the daytime than in the nighttime although the difference was marginally non-significant (nighttime: mean$\pm$SD$=4.20\pm$ 0.84: daytime: 6.29 ± 1.98, Mann-Whitney's U-test: $U=7$, $P=0.079$). In S1 type males and females, there were no significant differences in the number of mating individuals between the nighttime and daytime (S1 type, nighttime: 1.40 ± 1.52: daytime: 0.29 ± 0.49, Mann-Whitney's U-test: $U=10$, $P=0.167$; female, nighttime: 8.80 ± 2.49: daytime: 8.71 ± 2.29, Mann-Whitney's U-test: $U=17$, $P=0.933$). On the contrary, the number of mating S2 type males was significantly larger in the nighttime than in the daytime (nighttime: 3.60 ± 0.55: daytime: 2.14 ± 0.69, Mann-Whitney's U-test: $U=2$, $P=0.008$).

In several species of beetles, horn length or body size significantly affects the outcome of male–male competition for gaining access to resources (RASMUSSEN, 1994; EMLEN, 1997; MOCZEK & EMLEN, 2000; HONGO, 2003). Therefore, it is likely that larger males of *P. d. okinawanus*, which have enlarged mandibles, are stronger competitors than smaller ones. In the present field study, the number of observed individuals and mating individuals of L type males exhibited the maximum peak at 8:00 after the sunrise. Thus, it is inferred that there should be some benefits for L type males to appear at this time of a day. It has been known that in some plant species, such as tomato *Lycopersicon esculentum* the amount of sap transported from root to shoot is larger during the daytime than during the nighttime (CHOI *et al.*, 1999). This suggests that also in *C. trichotomum* var. *esculentum* and *P. thunbergii* the amount of sap exuding from the tip of branches may become largest at a particular time of a day. It is possible that the largest number of L type males were found at 8:00 because they monopolize good feeding spots at the best time of a day. Further studies on the timing of sap exuding in food plants of *P. d. okinawanus* in the Naha and Yanbaru populations would help to clarify the proximate factors of daily activity pattern of this beetle.

In several species of horned beetles, the existence of alternative reproductive tactics, that is, non-competitive tactics of competitively disadvantageous smaller males, has been reported (EBERHARD, 1982; GOLDSMITH, 1987; SIVA-JOTHY, 1987; EMLEN, 1997; MOCZEK & EMLEN, 2000). In males of *P. d. okinawanus* of the Yanbaru population, it has been reported that S1 type males came earlier to feeding spots and re-

mained later there than L type males to mate with females in the absence of L type males (SHIOKAWA & IWAHASHI, 2000 b). The present field observations in the Naha population showed that the number of observed L type males achieved the maximum peak in the daytime, whereas that of both S1 and S2 type males achieved the maximum peak in the nighttime. Furthermore, the number of mating L type males was highest in the daytime, whereas that of both S1 and S2 type males were highest in the nighttime, and frequency distributions of the number of mating individuals per two hours between L and S type (S1 & S2) males are significantly different (Kolmogorov-Smirnov test: $\chi^2=8.17$, $P=0.034$). These results suggest that S type males of *P. d. okinawanus* of the Naha population may also exhibit alternative reproductive behavior to gain access to females, although the temporal pattern of daily activity differs from that of the Yanbaru ones. It is likely that both S1 and S2 type males of the *P. d. okinawanus* of the Naha population avoid appearing at feeding spots when there are many L type males so as not to directly compete with them for mating.

Acknowledgements

I thank Drs. M. IMAFUKU and A. MORI (Department of Zoology, Graduate School of Science, Kyoto University) for their critical reviews of the manuscript and Drs. T. MIYATAKE (Laboratory of Animal Population Ecology, Faculty of Agriculture, Okayama University) and O. IWAHASHI for their helpful comments on early versions of the manuscript. I also thank Dr. T. SHIOKAWA and all colleagues of the Entomological Laboratory, College of Agriculture, University of the Ryukyus who helped my field research and laboratory experiments at that time. This work was supported in part by a Grant for the Biodiversity Research of the 21st Century COE (A14).

要　約

本郷儀人：日中に活動するオキナワノコギリクワガタ．—— 沖縄島に生息するオキナワノコギリクワガタのうち，島の北部に生息する個体群（ヤンバル個体群）における成虫では，これまでの研究により夜行性であることが報告されている．しかしながら，本種の南部における個体群（ナハ個体群）では，予備調査中に日中にも活動する個体が観察された．本研究では，ナハ個体群の成虫の一日を通した日周活動を，野外と室内条件下で調査した．その結果，野外では日中にも夜間と同レベルの活動が見られたのに対し，室内では日中の活動は夜間に比べて低かった．ナハ個体群がヤンバル個体群とは異なり，なぜ夜間だけでなく日中にも活動するのかについて，成虫の餌資源の観点から議論した．

References

CHOI, J. H., G. C. CHUNG & S. H. LEE, 1999. Influence of night humidity on the distribution of calcium and sap flow in tomato plants. *J. Plant. Nutr.*, **22**: 281–290.

EBERHARD, W. G., 1982. Beetle horn dimorphism: making the best of bad lot. *Am. Natural.*, **119**:

420–426.

EMLEN, D. J., 1997. Alternative reproductive tactics and male dimorphism in the horned beetle *Onthophagus acuminatus* (Coleoptera: Scarabaeidae). *Behav. Ecol. Sociobiol.*, **41**: 335–341.

FOSTER, S. A., & J. A. ENDLER, 1999. Geographic Variation in Behavior: Perspectives on Evolutionary Mechanisms. Oxford University Press, New York.

GOLDSMITH, S. K., 1987. The mating system and alternative reproductive behaviors of *Dendrobias mandibularis* (Coleoptera: Cerambycidae). *Behav. Ecol. Sociobiol.*, **20**: 111–115.

HONGO, Y., 2001. Bark-stripping behavior of male stag beetle, *Prosopocoilus dissimilis okinawanus* using mandibles. *Nat. & Ins., Tokyo*, **36** (3): 10–12. (In Japanese.)

——— 2003. Appraising behaviour during male–male interaction in the Japanese horned beetle *Trypoxylus dichotomus septentrionalis* (KÔNO). *Behaviour*, **140**: 501–517.

HORI, S., 1996. An Illustrated Guide to Okinawan Insect. Vol. II. [Okinawa Konchû Yagai Kansatsu Zukan] (Ed. 2). Okinawa Shuppan, Okinawa, (pp. 40–43). (In Japanese.)

KON, M., 1984. Swarming and mating of *Chironomus yoshimatsui* (Diptera: Chironomidae): seasonal change in the timing of swarming and mating. *J. Ethol.*, **2**: 37–45.

KREBS, J. R., & N. B. DAVIES, 1993. An Introduction to Behavioural Ecology (Ed. 3). Oxford University Press, Blackwell Science.

MOCZEK, A. P., & D. J. EMLEN, 2000. Male horn dimorphism in the scarab beetle, *Onthophagus taurus*: do alternative tactics favour alternative phenotypes? *Anim. Behav.*, **59**: 459–466.

OKAJIMA, S., & S. YAMAGUCHI, 1988. An Introduction to References of Stag Beetles [Kensaku Nyûmon Kuwagatamusi]. Hoikusha, Osaka. (In Japanese.)

RASMUSSEN, J. L., 1994. The influence of horn and body size on the reproductive behavior of the horned rainbow scarab beetle *Phanaeus difformis* (Coleoptera: Scarabaeidae). *J. Ins. Behav.*, **7**: 67–82.

SHIOKAWA, T., & O. IWAHASHI, 2000 a. Mandible dimorphism in males of a stag beetle, *Prosopocoilus dissimilis okinawanus* (Coleoptera: Lucanidae). *Appl. Ent. Zool.*, **35**: 487–494.

——— & ——— 2000 b. Mating success of small sized males of Japanese stag beetle *Prosopocoilus dissimilis okinawanus* NOMURA. *Jpn. J. Ent.*, **3**: 157–165. (In Japanese with English abstract.)

SIVA-JOTHY, M. T., 1987. Mate securing tactics and the cost of fighting in the Japanese horned beetle *Allomyrina dichotoma* L. (Scarabaeidae). *J. Ethol.*, **5**: 165–172.

YOSHIMOTO, J., & T. NISHIDA, 2004. The effects of carpenterworm (Lepidoptera: Cossidae) on tree sap exudate and the attracted insect community. Abstr. 48 Annual Meeting Appl. Ent. Zool., Kyoto. 32 pp. (In Japanese.)